BIOLOGICAL AND SYSTEMATIC PROBLEMS INVOLVING SOIL DWELLING ARTHROPODS

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ABSTRACT

Study of structure, classification, and way of life of myriapods is still in a threshold position, and ground is being lost rapidly because current researchers are not only numerically fewer than in the past, but are less productive. Ironically, at the same time, their research potential is becoming appreciated, and a rapidly increasing interest in these animals is being shown by ecologists and other biologists. Regrettably, a number of important major discoveries in myriapod biology during the past 30 years have been left fallow, after their discoverers died or turned to other subjects. The present deficiency in alpha *and* beta *taxonomy has had a negative effect on other areas of research: it is not very useful to investigate organisms which are nameless and unclassified. The obvious solution to the problem is to increase the number of systematists and provide the necessary outlets for major revisionary studies. If necessary, funds should be diverted from well-known but still intensively studied groups like terrestrial vertebrates and angiosperma, and allocated to inadequately known and even less-studied organisms of the soil, on which all terrestrial life ultimately depends.*

RÉSUMÉ

Certes on a souvent dit que la taxonomie, la morphologie et l'histoire naturelle des Myriapodes sont encore dans leur enfance, et que ces domaines prennent même actuellement du recul parce que les chercheurs y sont moins nombreux et moins productifs que par le passé. Ironiquement par contre, les écologistes et aurtes biologistes montrent un intérêt croissant pour ces animaux, dont ils realisent le potentiel en matière de recherche. Il est fort regrettable que plusieurs percées importantes dans l'histoire naturelle des Myriapodes ayant eu lieu au cours de 30 dernières années n'aient point connues de suite après que leurs découvreurs soient décédés ou aient changé de champ d'étude.

La déficience actuelle en taxonomie alpha et bêta a évidemment un impact négatif sur les autres domaines de recherche: il n'est pas très utile d'étudier des organismes qui ne sont ni nommés ni classifiés. La solution évidente à ce problème est d'augmenter le nombre de systématiciens etudiant les Myriapodes et d'offrir les debouchés nécessaires pour d'importants travaux de révision taxonomique. Si cela s'avère nécessaire, des argents supportant présentement des travaux sur des groupes bien connus mais malgré cela encore sur-étudés, tels que les Vertébrés et les Angiospermes, devraient être redistribués pour soutenir des projets d'étude de groupes mal connus et encore négligés d'organismes du sol, desquels dépend ultimement le maintien continu de toute vie terrestre.

INTRODUCTION

It is common for scientists in virtually any discipline, no matter how sophisticated it may have become, to deplore deficiency of knowledge in their specialty. I suspect, however, that the participants in this symposium are, by virtue of their own experience, disposed to accept a general *apologia* that existing knowledge about myriapods is strickingly deficient and fragmentary. It is certainly not an overstatement to note that myriapodology – and such a word

is not even in dictionaries – is presently at the same level of development as was entomology about 1850, or ornithology about 1800.

Many persons whose knowledge of Myriapoda derives from standard texts published in the recent past, consider this group to include few orders of insignificant classes, and are surprised to learn that diplopods alone constitute 15 orders and about 115 families. There is more to the subject than *Julus*, *Spirobolus*, and *Lithobius*, and the major problem that I had to face on being invited to summarize current "state of the art" for the four myriapod classes was how to do it meaningfully in 30 minutes. I have little confidence that such a goal can be achieved, even with rather superficial coverage. Three areas will be considered: present state of knowledge of myriapods; problems impeding an improved knowledge of them; and what is presently known about the impact of myriapods on the formation and characteristics of soil. Even for inadequately known taxa, this is a large order.

PRESENT STATE OF KNOWLEDGE OF MYRIAPODS

Systematics

To begin with, even the phylogenetic relationships of the classes Diplopoda, Chilopoda, Pauropoda, and Symphyla to each other and to the hexapod tracheates are far from being established. Much has been written on this point since about 1887, when R.I. Pocock established the first "modern" arrangement, aligning Diplopoda, Pauropoda, and Symphyla in a group Progoneata, and the Symphyla and Insecta in the coordinate Opisthogoneata. The most extensive recent work, and by far the most authoritative, has been that of S.M. Manton whose approach to the postulation of phylogeny was based largely upon comparisons of structural and functional aspects of locomotory systems. Without wishing to denigrate in any way the superb research conducted and published by Manton (1954–1977) with exceptional illustrations, I feel that her conclusions were seriously flawed by reliance upon an outdated classification (that of Attems, 1926, which was actually written near 1920), and by insufficient consideration of adaptive convergences. In particular, I cannot accept the notion that "myriapods" comprise a monophyletic entity coordinate to a comparable "hexapod" group as separated solely by a difference in mode of mandibular articulation. Single character differences between taxa do not inspire much confidence when they oppose groupings made on the basis of extensive similarities in numerous character-systems. I prefer to recognize an indivisible spectrum of tracheate classes, which awards class rank for collembolans, proturans, diplurans, thysanurans, and pterygotes, and which admits the numerous shared characters of diplurans and symphylids. I am not aware at the present of any convincing arrangement of these five hexapod and four myriapod classes into higher groups (*e.g.*, superclasses or subphyla). Depending on which character systems are stressed, any number of classifications could be devised, including one that sets Diplopoda apart in a sister-group relationship to the other eight combined. The fossil record has, so far, shed very little light on this problem.

Initially, "myriapods" were studied by general zoologists, then – up to about 1900 – by entomologists. The primary taxonomic characters of both pauropods and symphylids are chiefly those of chaetotaxy and subtle modifications of the integument, and except for the advantage of improved optical equipment, the techniques involved in their study have changed but little in the past century. Similarly, the study of lithobiomorph and scolopendromorph chilopods still follows classical procedures of the last century (enumeration of spines, spurs, and sutures). But a fundamental change occurred in classification of geophilomorph centipedes around 1870, with Meinert's discovery that the best familial and generic characters reside in mouthpart

structure. This realization instantly rendered all previous work on these animals obsolete, and mandated the eventual restudy of early geophilid types. A similar revolution in milliped classification was triggered in 1884, when Robert Latzel made extensive and effective use of male genitalia to distinguish both genera and species in the central European fauna. Genitalia had been sporadically described, and even illustrated, since 1832, but Latzel's consistent and comprehensive emphasis of these appendages was catalytic. Virtually all millipeds named prior to Latzel's time require redescription with respect to genitalic structure.

As the result of these important discoveries by Meinert and Latzel, generation of myriapod specialists emerged around 1890, some of its members being converted entomologists, some innocent of any previous tradition. A cadre of six dynamic young men working chiefly in the 1890s built the foundations of our existing classifications of the various myriapod groups, except for the Pauropoda and Symphyla. Working most of the time in isolation, some of them adopting inappropriate attitudes about taxonomy and nomenclature, they also provided a heritage of confusion, duplication, and outright systematic anarchy that by 1950 had attained epic proportions. Most of these pioneers endeavored to study the world fauna of both chilopods and diplopods (often the other two classes as well), and if their work was adequate in one class, it was usually catastrophic in the other. Recitation of the problems generated during this period would fill a volume, and a large part of modern work consists of tedious corrective surgery.

During this period, about 60 years in duration, of intense descriptive work, emphasis was placed on alpha taxonomy of the crudest sort, usually the naming of material in regional collections. Some of the most productive workers seemed to operate on the principle that the mere naming of taxa, without a word of comment, was the pinnacle of taxonomic achievement. It was not until the global catastrophe of World War II that this period came to an end, coincidentally with the demise of most of its major figures.

To illustrate the rather spectacular growth during this period I can provide two illustrations from the Diplopoda, the group I know best. The first is a table of higher taxa recognized at various time intervals from 1847 to the present. The figures are not absolute, as they do not take into account existing taxon names regarded as synonyms by the various authors cited.

Another way to show the same trend is with a line graph (Fig. 1) showing the increase in number of generic names cumulatively, without prejudice as to their actual status.

The almost explosive increase, beginning in the 1890s, is not much different from that in other major taxa, but begins much later than most, and represents the astonishing productivity of three persons: Carl Attems, K.W. Verhoeff, (1926–1932), and R.V. Chamberlin, who among them proposed no fewer than 1199 genera. One notices that the curve begins to level off after 1950, but this is purely a result of changing times and not a depletion of undescribed genera. Actually, two things have conspired to dampen the growth rate. First is a post-war change in taxonomic philosophy, from sheer mindless description of novelties as an end in itself to a strong emphasis on clean-up work: restudy of old types, preparation of whatever revisions could be managed, and so on. Second, and perhaps more compelling, has been the incredible increase in the costs of publication. (In these days of near-universal page-charges, it is refreshing to recall that Verhoeff, for instance, was actually paid – so many words per mark – by the *Zoologischer Anzeiger* and other German journals. Today only a millionaire could afford to publish the typical Verhoeffian output of several hundred pages per year.)

I believe that we have so far described about 20% of the actual milliped fauna of the world. If this figure be true also for the other three classes, a sum total of more than 100,000 myriapod species must be reckoned with.

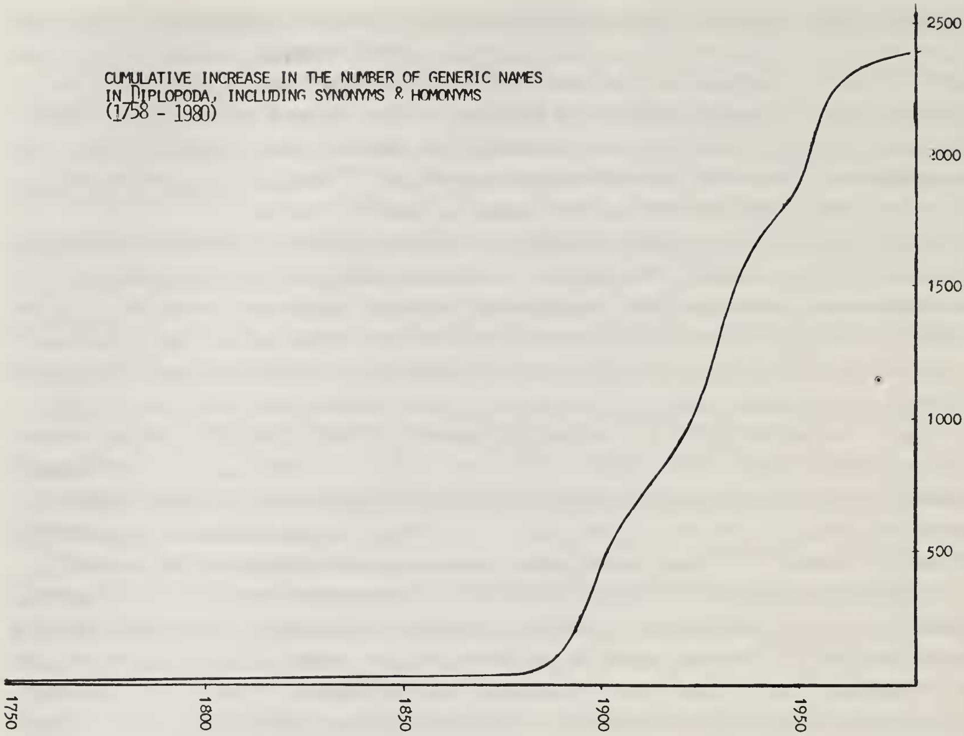

Fig. 1. Cumulative increase in the number of generic names in Diplopoda, including synonyms & homonyms (1758–1980).

Table I
Increase in the number of higher taxa, Class Diplopoda

Reference	Orders	Families	Genera
Gervais, 1847	1	5	16
Bollman, 1893	4	7	60
Cook, 1895	6	50	190
Silvestri, 1897	6	66	353
Attems, 1926	7	70	621
Hoffman, 1980	15	115	1701

The only comprehensive treatment of the classfication, structure, and way of life of all four classes is that of Carl Attems, in the Kükenthal-Krumbach *Handbuch der Zoologie* (1926), which was written more than 60 years ago. The taxonomic part is of course hopelessly out of date, and was seriously flawed even at the time it was written, but for many taxa it still remains the only existing reference.

For Diplopoda, two recently published manuals are useful. One is a catalog of all generic and familial group names, with their type species, published from 1758 to 1957 (Jeekel, 1971). The other is a classification of the world fauna down to the level of subgenera, compiled by me (Hoffman, 1980). It contains no keys nor descriptions, but does include reference to all post-1926 synoptic taxonomic papers.

The enormous order Polydesmida was surveyed by Attems in three big volumes of the *Tierreich* series (1937–1940), but these works are chiefly useful from a bibliographic sense, being mostly compilations severely handicapped by their author's ultraconservative taxonomic philosophy. At least all polydesmoids described up to that time are included somewhere, and Attems' real contribution was to provide a beachhead for further, more refined studies. In recent years, some work, reminiscent of the labors of Hercules, has been conducted by a few hobbyists. The Paradoxosomatidae, largest family of the entire class, has been under study by C.A.W. Jeekel since about 1950. This author published a provisional classification of the group in 1968, as well as numerous generic synopses and clarifications of nomenclature, but his intended goal – a new revision of the entire family – is still a long way in the future. Since about 1955, I have been working in a similar way on the larger chelodesmoid families, *e.g.*, the Chelodesmidae, Oxydesmidae, and Gomphodesmidae. Although revisions of many genera and tribes have been published, only the African family Oxydesmidae is now actually at the stage of preparation for publication. The Chelodesmidae will doubless prove to be the largest family of Diplopoda: already more than 20 tribes and 200 genera have been defined even though the fauna of Brasil has scarcely yet been sampled. The family Xystodesmidae, virtually endemic to North America, is being worked up one genus at a time, beginning with the rich Appalachian fauna, by R.M. Shelley (*e.g., Sigmoria*, 1981). But the numerous families of "smaller polydesmoids" have received essentially no attention and at present nobody has either the time or interest to study them despite their importance in soil samples from any tropical region.

In the order Chordeumatida, characterized by a large number of mostly small disjunct families, some progress has been made chiefly on the Nearctic fauna by W.A. Shear, who has revised the Conotylidae (1971), the Cleidogonidae (1972), Rhiscosomididae (1973), and Tingupidae (1982). Dr. Shear advises me, however, that in less than a decade so much new material has accumulated as to render his cleidogonid monograph obsolete. Other students of this order, notably S.I. Golovatch and J.–P. Mauries, have published descriptive papers on the Old World fauna but do not appear to be contemplating comprehensive revisions. The study of this order is greatly impeded by the scarcity of material; a great many species still remain known only from the type series named decades ago.

The large, mostly tropical species of the order Spirostreptida have been recently, and adequately, summarized: the Spirostreptidae itself by Krabbe (1982), the Harpagophoridae (in part) by Demange (1961 *et seq.*), and the Odontopygidae by Kraus (1960, 1966). These large and useful papers go far to setting in order the classification of the three families, but still represent only a first step, and none of the many genera involved have yet been the subject of a "modern" revision. The cambaloid members of this order remain in a state of substantial confusion, with little agreement even about the definition of families, but the group is being

studied by Mauries and it is hoped that a revisionary monograph may be forthcoming in a few years.

Species of the related order Julida remain in a sort of limbo. The family Parajulidae, which is virtually endemic to North America, was studied for many years by N.B. Causey, but despite appreciable research nothing useful was published before Dr. Causey's death in 1979, and no one has touched the group since. A more optimistic statement can be made about other juloid families, which are now being investigated by Henrik Enghoff. It is the intention of Dr. Enghoff to eventually reorganize the classification of the entire order, and toward this end a number of preliminary studies have already been published.

Lastly, in the order Spirobolida, the family Spirobolidae was monographed in a very adequate way by W.T. Keeton in 1960. This group is in a good condition for detailed biosystematic studies of individual genera. The other spiroboloid families – such as have been adequately defined – remain in complete chaos, and identifications of rhinocricids, pachybolids, and trigoniulids are virtually impossible to make.

Many families, especially in the Palearctic region, are monobasic or nearly so, and their revision would entail only careful studies of structural features and comparisons with related taxa. Omitting such groups, and in summary, less than 10 families of Diplopoda have been recently treated taxonomically in a way useful to beginners, *e.g.,* with keys, diagnoses, illustrations, synonymical lists of species, maps, and other features normally taken for granted by students of most other animal groups.

From a faunistic standpoint, the record is not much better. Checklists are available for North America (Chamberlin & Hoffman, 1958) and Mesoamerica (Loomis, 1968); both are not considerably outdated. National surveys are available for Great Britain (Blower, 1955, and in press), Germany (Schubart, 1934), France (Demange, 1981), India (Attems, 1936), and Japan (Miyosi, 1959). One of the best-known parts of the world for diplopods is the Union of South Africa, thanks to the work of Attems (1928, 1934), Schubart (1956, 1958, 1966), and Lawrence (numerous papers, *e.g.,* 1953a and b, 1967). A few unlikely parts of the world have been treated faunistically, such as the island of Hispaniola (Loomis, 1936) and Panamá (Loomis, 1964).

Centipeds are probably even more inadequately-known than millipeds. A catalog of generic names and their type species has been compiled by C.A.W. Jeekel but not yet published, and there is no classification of the Chilopoda *in toto* since 1926. The order Geophilomorpha was treated in the *Tierreich* series by Attems (1929) and the Scolopendromorpha by the same author a year later (1930). Aside from being decades out of date, both of these manuals were largely compiled from faulty literature and were inadequate the day they were published. The content of both orders has virtually doubled in the past fifty years, with no reliable update. The enormous and difficult order Lithobiomorpha has not been treated comprehensively, nor has the much smaller Scutigeromorpha.

Regional papers have been published for Great Britain (Eason, 1964), France (Brolemann, 1935, Demange, 1981), and South Africa (Attems, 1928). The Lithobiomorpha of the Soviet Union was treated by Zalesskaja (1978) and the North American species of this order were covered in an excellent series by R.V. Chamberlin (1913–1925). Unfortunately, the good start embodied in the last-cited reference was promptly subverted by a long sequence of unsatisfactory "descriptive" papers by the same author during the following 30 years. The often cryptic synonymy and nomenclature of lithobiids has been clarified over a period of time by E.H. Eason, who hopes to prepare a world catalog for this large and difficult family. A good

start was made toward reclassification of Geophilomorpha by R.E. Crabill during the years 1960–1968, but regrettably no major synthesis was published before his retirement in 1983. Recent, outstanding work on this order is being published by L.A. Pereira, who expects to revise initially the family Schendylidae, and eventually other geophiloid taxa as well. The chilopod fauna of southern Europe, particularly Italy, is being studied by A. Minelli.

No optimistic statement can be made about the classes Pauropoda and Symphyla. At present, both of them are virtually the exclusive domain of Ulf Scheller. The scarcity of good material in both groups, and the very fragmentary geographic representation, renders revisionary studies almost impossible. Scheller's faunistic studies, however, are models of excellent presentation and include as much group taxonomy as can be managed. So many pauropods are cosmospolitan or nearly so, that a world synopsis of this class is necessary for adequate work, and at present this can be gained only by knowledge of the entire published taxonomic literature in the original. It is possible that Dr. Scheller will prepare a catalog of the species of one or both classes.

Concluding this somewhat discouraging summary of myriapod classification at the present time, a glance at the number of current active specialists cannot fail to give an even gloomier prospect for the future:

Chilopoda: England, 2; France, 2; Italy, 1; Australia, 1; Argentina, 1; U.S.S.R., 2; total: 9.

Diplopoda: U.S.A., 3; France, 2; Denmark, 1; Germany, 1; U.S.S.R., 2; Japan, 2; Holland, 1; total: 11, two of which are duplicated in the chilopod list.

Pauropoda: Sweden, 1; Austria, 1; Germany, 1.

Symphyla: Sweden, 1.

Most of the foregoing specialists are either teachers or curators; in either case, their research time is limited (or outright stolen from primary obligations). Nearly half of them are nearing the end of their productive years. All are innundated with material, and years behind on projects and gratuitous identification work. At most, only about five persons are relative newcomers to myriapod taxonomy.

Morphology

What can be said of taxonomy's sister science, morphology? Outstanding anatomical studies have been made in recent years by Demange and by Manton. The latter author dealt primarily with integumental and musculature modification associated with locomotion. Demange published an outstanding study on thoracic segmental musculature in 1967, with many profound implications (some of them controversial). I do not know any subsequent researches extending, confirming, or refuting the findings of these two pioneers. It cannot be said that the study of even the general aspects of structure of myriapods has been exhausted, and I cite a few examples. (1). A good comparative study of the head capsule amongst diplopods has not been published, nor has an attempt been made to homologize head musculature with that of body segments. (2). Species in several spiroboloid families have paired paramedian dorsal pits on each segment, of totally unknown function. (3). In the family Paradoxosomatidae, many species have glands opening through paired pores on the 5th sternum: such glands have not been mentioned by anybody and I suppose have been overlooked to the present. Obviously their function likewise remains unknown!

For Chilopoda, at least, the areas of ignorance have been categorized in Dr. John Lewis's recent (1981) book on centiped biology; someone seeking structural, developmental, or ecological problems can find one on nearly every page. Some come at once to mind. (1). Many

geophiloids have conspicuous sclerotized sternal pits, much used in taxonomy but of totally unknown function. (2). What is the function of the Tömösvary Organ? (3). What is the function of coxal pores in lithobiomorphs?

Only within the past two decades has anything been done of note with the neurosecretory structure of centipeds (or millipeds, for that matter). The same time period has seen the initiation of work on microstructure of muscles, of sperm cells, of sensory organs. As many as a dozen papers have been published in these areas. But since something has to be skimmed over in this review, the cut is in structure: there is much to cover yet.

Embryonic development of millipeds was first studied in the last century by Metschnikoff, Newport, and Heathcote. Several papers were published by Silvestri (*e.g.*, 1950), Pflugfelder (1932), and most recently and thoroughly, by Dohle (1974). Details of development for many orders remain unknown, including those for the exceptional group Stemmiulida in which the young eclose with 19 segments instead of the six common to all other diplopods. Demange has observed that embryos of most groups reveal little information about phylogeny because many critical structures do not appear in the early stages. Yet, there is plenty of opportunity for a student to make a distinguished career in this area.

Much happens after hatching. In many milliped groups, the male genitalia begin to modify from normal walking legs early in the stadium sequence, becoming larger and more specialized with each moult. In polydesmoids, however, the final moult changes a small knob-like primordium into a mature gonopod of often fantastic complexity. Nobody has sectioned specimens during this diapause period to follow the sequences of events, to determine what pattern may exist comparable to the mechanisms that direct the reorganization of holometabolous insects during pupation. Development of the modified posteriormost legs of male lithobiomorph centipeds has not been studied, either.

Way of Life

The foundations of present knowledge about myripod way of life were laid down chiefly by K.W. Verhoeff, who studied the Palearctic fauna for half a century. Verhoeff (1926–1932) worked out the life histories of many kinds of millipeds and centipeds, and discovererd the interesting phenomenon that occurs in various kinds of julids: non-mating intercalary adult males ("Schaltstadium") which moult into a sexually active stage. This subject has been carefully studied in England by J.G. Blower and some of his students, and in France by F. Sahli (*e.g.*, 1969). In general, postembryonic development, particularly of julids, occurs in a number of remarkable patterns, in many taxa with stadia omitted or added. Blower's group has also worked on population structure, phenology, and general natural history of various British millipeds, and provided a fine model for those who might wish to study the fauna of other regions (*e.g.*, Blower & Gabutt, 1964; Blower & Miller, 1974). Fundamental work on way of life of *Ommatoiulus moreleti*, an Iberian julid introduced into South Africa and Australia, is being conducted by G.H. Baker (1978a-c).

Details about life history have been published for only two North American millipeds (and no centipeds), and these are not comparable to the precisely executed studies of European investigators. A few papers have referred superficially to habitat preferences of American species, contrasting with the careful work of J.–J. Geoffroy (1981) on the French fauna. Interactions of myriapods with other organisms and with their environment have rarely been better-accounted than in R.F. Lawrence's notable book about South African soil fauna (1953).

Diplopods were considered to practice only the most perfunctory kinds of reproductive behavior. During the past two decades, publication by Ulrich Haacker (1969), in Germany, reported fairly sophisticated courtship practised by some julids, the males of which preferred an attractive secretion from the base of the 2nd pair of legs, which attracted (and distracted) females which fed upon the material whilst the male inobstrusively effected copulation and sperm transfer. Haacker (1971) also reported apparently similar glands located middorsally on the terga of several European chordeumatids, but was not able to observe their actual use. In other studies (1968) he taped and analyzed the stridulation of South African sphaerotheriids, produced by males as an element in courtship. Lamentably, this gifted investigator died at an early point in his career, and nobody has since continued along the trail he blazed so well. Regrettably, detailed studies of reproduction have not been reported for a single North American milliped. The considerable body of published field and laboratory observations has not been organized for second-stage, follow-up work. One facet that merits careful study is the sociality of platydesmid species, represented most conspicuously in the United States by the genus *Brachycybe.* These animals tend to live in large aggregations of all stages, and in such colonies specimens are often seen in a stellate arrangement, heads together, bodies radiating out like spokes, for a still-unknown reason. In this genus, large numbers of tiny yellow eggs are released by the females, then gathered up and brooded by males, an exceptionally rare occurrence among anthropods. The phenomenon was observed by me in North Carolina in the summer of 1958; by an astonishing coincidence it was published in the same year by Y. Murakami for a Japanese species of *Brachycybe.* Careful studies remain to be made for other platydesmid genera in North America and the Mediterranean region. Do they share this trait? How could such deviant behaviour have developed?

Males of many diplopod taxa, particularly polydesmoids, are provided with a complex arsenal of secondary sexual modifications of legs, sterna, and mouthparts. How such equipment is used remains completely unknown, and could be elucidated by just the simplest observation of mating pairs. Some is obviously involved in clasping the female, some, involving internal glands and their pores, must perform an attractant function. Mauries (1969) described the mating behaviour of *Typhloblaniulus lorifer*, in which coupling and positioning of the female is achieved by intertwining of the bodies, by the female biting the modified 1st legs of the male, and by the female's antennae being clasped by a modification of the male's mandibles. Species of the allied family Parajulidae occur in abundance over much of North America, adults exhibit a wider variety of sexual modifications, and yet not a single observation has been published on reproductive aspects of this big family. There is also a capital problem involving *Aenigmopus alatus*, Guatemalan polydesmoid males, which lack gonopods: how does it accomplish sperm transfer? This species is known so far only from type material, but a precise locality is known and it should be possible to obtain living specimens.

Prior to about 1957, virtually nothing was known about the mating behaviour of chilopods. Using infra-red light for observations, H. Klingel solved this riddle and reported his findings in several papers (*e.g.*, 1957, 1960). Apparently little has been done since that time. It is well-known that the males of numerous American lithobiomorph genera have the last pair of legs modified in curious ways: a spectrum of knobs, crests, cavities, hair tufts, and pore fields. Could not some student of behaviour adopt Klingel's techniques to see what role these strange modifications play in mating? Do females recognize corresponding males tactily?

It has been known for years that millipeds produce a variety of caustic and/or aromatic secretions when disturbed, the odours being variously reported subjectively as like camphor,

almond extract, osmic acid, quinine, creosote, and rotting sponges. A few chemical analyses were made during the first half of this century, but scientific studies on allomones were really first initiated by Thomas Eisner about 25 years ago. Eisner investigated not only the chemical composition of these secretions but their biological functions as well. Aside from the obvious role of predator deterrents, most of the secretions are markedly fungicidal, suitable for organisms which live in damp biotopes (Eisner, 1970). The structure of the ozadenes was worked out by D.W. Alsop in Eisner's laboratory, but details have, to the best of my knowledge, not yet been published. Biosynthesis of benzaldehyde and hydrogen cyanide, common ingredients in polydesmoid allomones, was worked out by Duffey, Underhill & Towers (1974) in *Harpaphe haydeniana*, a common species in British Columbia. Substantial progress was made at the University of Georgia (cf. Duffey, 1977) toward possible chemotaxonomic use of allomones, but once again, a promising start soon faltered and nothing is currently being done along these lines. Existing evidence suggests a fairly close correlation between allomone structure and established taxonomic groups.

Some millipeds are known to be luminescent, a phenomenon especially well developed in some Californian xystodesmids, reported by Davenport (1952), but with inconclusive evidence about the cause. Some geophilomorph centipedes emit a phosphorescent secretion from sternal glands, but to what end remains unknown. Most geophilomorphs are some shade of yellow, brown or red. The small species of the tropical family Ballophilidae, however, depart from this norm in their colouration: bright blue, violet, purple, green, and black species are known. Ballophilids are characterized in part by having the sternal glands open onto a midventral sternal knob, and in fresh specimens the glands can be easily seen as clusters of intense pigmentation through the more dilute colouration of the integument. What is different about ballophilids and their sternal glands? No one has any idea. Not even the crudest histochemical assay has yet been attempted.

The foregoing enumeration of some areas of ignorance has largely avoided mention of either pauropods or symphylids. It is hardly necessary to add that virtually nothing is known about the structure and way of life of members of more than one or two common European species.

IMPEDIMENTS TO DEVELOPMENT OF MYRIAPODOLOGY

I am sure that those who study mites, nematodes, springtails, or pseudoscorpions will be surprised at little I have said so far: most soil organisms share this heritage of neglect. No doubt all of us tend to agree that problems such as the following are serious ones:

1. Virtual ignorance of the actual fauna in many parts of the world, especially the tropics, and frequently there is a burden of inadequate taxonomic and complex nomenclatorial problems afflicting even the better-known faunas.

2. The likelihood that major parts of the world's soil fauna will become extinct before it can even be sampled. Berleseate samples now in dead storage in various museums probably contain a number of already extinct species: fossils in alcohol.

3. Difficulty of entry into the classification and identification of most groups because the literature is extensive, fragmentary, widely scattered, and polyglot.

4. The frequent impossibility of obtaining identifications because either there are no specialists, or, if such exist, they are 35 years behind their unidentified backlog, or, worse, unable to make an identification without having first to revise the genus, tribe, or family involved.

I may be forgiven my bias in believing that organisms must be described and placed in a classification before information about them is meaningful. Taxonomy may be *passe* in ornithology and some other mature fields of zoology, but I am appalled to observe how many people are still investing vast resources of time and money deciding whether a given vertebrate taxon is a good species, a sibling species, a subspecies, or what, when the majority of arthropods are still unknown, uncollected, and ignored. Is it a better investment to investigate details in vertebrates, or get on with the higher classification of other phyla?

Solutions are fairly obvious. Most of the present generation of myriapodologists drifted into this area accidentally, and remained in active pursuit of research goals primarily as a personal hobby, with time abstracted from career requirements and family obligations. Even museum curating is no ideal occupation, if one is primarily responsible for the collections first, routine identifications second, and perhaps personal research last. If more taxonomists are needed to handle the job of working up what we have already in museum jars, some better way must be found to employ their talents on an occupational basis. What graduate student wishes to invest quite some years in learning the complexities of myriapod lore, if there is no hope whatever for finding gainful employment in such a specialty? Research on structure, behaviour, and ecology can be left to academic sectors. These are areas which can be rather quickly comprehended, pursued, and solved in segments by graduate students. Systematic work, in my view, requires a far longer time to master, and productivity is linked with continuity. I began the study of millipeds as an undergraduate, as did several of my friends, but could not do so today simply because I could not cope with publication problems. If progress is to be made in myriapod taxonomy not only must career opportunities be guaranteed, but possibilities for publication of taxonomic monographs must also be improved. Many of the better–known research–support sources (I may mention the U.S. National Science Foundation) award grants on an egalitarian basis: as much is given for studies of vertebrates (less than 1% of animal creation) as for arthropods (more than 90%). Is it possible to redistribute the available largesse on a scale commensurate with the actual size of the group, and its need for study? I strongly support the principle of peer evaluation of research proposals, but appeal for reason in the process. I have known excellent, deserving projects turned down because one or two reviewers felt that the applicant should have introduced reference to "phenetics" or "cladistics" or some other popular fad. In work on many groups of arthropods, we are still trying to scramble into the lower levels of *beta* taxonomy. We must crawl before we fly, and to impose a requirement for theoretical biology when there is no existing base for it, seems entirely unrealistic and counter-productive.

MYRIAPODS AND SOIL

Lastly, it is necessary to append a few remarks appropriate to the subject of this conference. I have investigated the historical background as far as the paper by Shaler, which first suggested a substantial role of diplopods in soil formation; also the classical texts written or edited by Kevan, Raw, and Schaller, also recent papers by van der Drift, Gere, and other European workers. Most publications so far relate to diplopods, and are in two categories: some subjective field observations lacking quantitative controls; and laboratory experiments not closely associated with natural conditions.

Two areas of actual soil influence are generally accepted: physical and chemical. The first involves disruption of the upper layers of soil and the litter accumulation by burrowing activities of diplopods. Many of these (which may be surface or even arboreal dwellers when

mature) may spend all of their immature stadia burrowed fairly deeply in the soil itself: the general collector rarely finds young millipeds in the upper horizons. Scolopendromorph and geophilomorph centipeds likewise burrow to some extent, or exploit the burrows of other animals. I think that either exclusively edaphic residence, or vertical circadian movement must be accounted a substantial influence on the physical makeup of upper soil strata, although I do not know of any work quantifying the effect. It is well-known, secondarily, that most millipeds are detritivores and break down a lot of vegetable material (leaves, rotting wood, fungi) simply by mechanical trituration as they feed upon it. Some earlier authors (Romell, 1935; Eaton, 1943) implicated millipeds as a major factor in mull formation, and certainly captives are able to reduce a handful of decomposing leaves in short order, as can be confirmed by anybody who keeps a live spirobolid under observation. But I am often amazed to sift through really large quantities of leaf litter in apparently optimal situations without finding a single milliped of any species, and humification proceeds apace. So far as I know, all chilopods are carnivores, and pauropods and symphylids probably poelomicrophaghes; these groups probably contribute very little to mechanical litter conversion.

Chemical influences are of several kinds: modification of plant material through digestion; uptake and concentration of calcium and other minerals; release of nitrogenous compounds from metabolic excretion; and formation of weak organic acids as the result of death and protein breakdown. Most of these factors have been alluded to qualitatively in the literature, but I have nowhere found quantitative studies aside from some experiments on mineral cycling at Oak Ridge, Tennessee, by Reichle and collaborators (1965).

One possible influence of a chemical nature was suggested by O.F. Cook in 1911, but not apparently considered by anyone subsequently. Cook, who was by profession an agricultural botanist, believed that the allomones produced by many millipeds were capable of altering soil composition by precipitating colloidal substances in the humus. He claimed, from personal observations, that " ... African forests have very slight superficial accumulation of dead leaves and humus. The soil remains relatively open and noncolloidal, and is inhabited by numerous species of millipeds. In the forests of tropical America ... the underlying soils are generally much more colloidal than in Africa and the milliped population is generally sparse, or often lacking altogether ... ". I pretend no knowledge whatever of this aspect of soil structure and present Cook's views here solely to give them circulation.

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